Master's thesis

NTNU
Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

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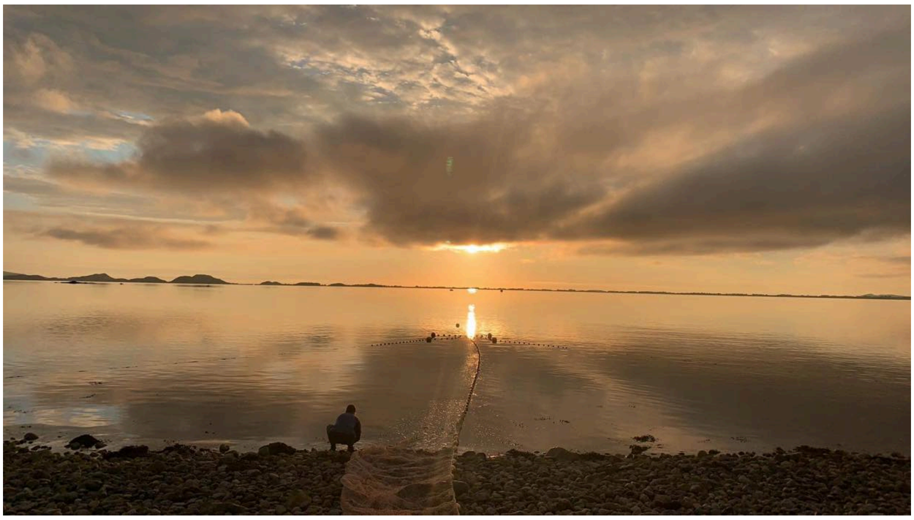
FACTORS REGULATING THE RETURN MIGRATION OF SEA TROUT (*SALMO TRUTTA*) IN RIVER FREMSTADELVA

Master's thesis in Ocean Resources
Supervisor: Bengt Finstad
Co-supervisor: Ingebrigt Uglem, Rachel Paterson
May 2021



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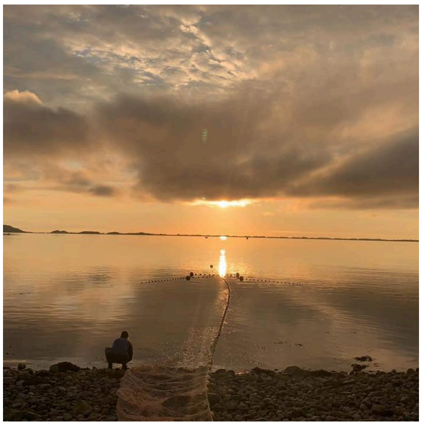

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ABSTRACT

While the impact of sea lice infestations on wild Atlantic salmon (*Salmo salar*) is being used as a sustainability indicator in the Norwegian management system, Trafikklyssystemet, more knowledge regarding the migration behavior and the marine habitat of anadromous sea trout is needed to implement lice infestation of anadromous trout as a sustainability indicator. In order to investigate factors regulating the timing and pattern of the return migration from the sea to freshwater, 191 brown trout post-smolts and veteran spawners were tagged with PIT-tags outside the Norwegian river, Fremstadvassdraget. In total, 63 of the sampled trout (33 %) returned to the river at the end of the marine growth phase. The length of the fish was found to increase the likelihood of a trout returning, possibly due to a reduced predation risk as larger trout are more powerful swimmers. Trout suffering severe infestation rates above 0.45 lice g^{-1} of body mass when they were tagged did not return, indicating that an increasing infestation rate reduce the likelihood of a trout returning. This thesis shows that these types of studies can be useful to define thresholds for when the sea trout do not return after the marine growth phase based on sea lice infestation rates. However, it is necessary to repeat these studies over several years for multiple populations. The majority of the fish returned during a water temperature range of 11 – 14 ºC in the estuary, perhaps due to a trade-off between the optimal temperature of growth and energy utilization, or possibly due to a seasonal effect. Most of the trout were also found to choose high tidal levels for the timing of the migration from the sea to the river as it may reduce the accessibility for terrestrial predators, as well as it may allow for more maneuverable water masses for the trout when it ascends the river. This thesis shows that abiotic conditions in the estuary may regulate the timing of the return from sea to freshwater, thus providing new insight for future studies aiming to answer questions related to the migration behavior of returning sea trout.

SAMMENDRAG

Til tross for at luseinfestasjoner på vill Atlantisk laks (*Salmo* salar) i dag brukes som en bærekrafts indikator i det norske forvaltnings systemet, Trafikklyssystemet, behøves mer kunnskap om ørretens vandringsatferd samt bruken av det marine habitat kreves for å implementere lusetrykk på sjøørret som en velferdsindikator. For å undersøke ulike faktorer som regulerer returneringstidspunktet fra sjø til elv samt atferdsmønsteret, ble 191 ørret postsmolt og flergangsgytere merket med PIT-tagger utenfor den norske elven, Fremstadvassdraget. Totalt, 63 av den merkede ørreten (33%) returnerte til elven mot slutten av den marine vekstfasen. En større kroppslengde økte sannsynligheten for at ørreten returnerte, trolig på grunn av redusert predasjonsrisiko ettersom større ørret er bedre svømmere. Ørret med alvorlige luseinfestasjoner over 0,45 lus g^{-1} kroppsmasse da de ble merket, returnerte ikke, noe som indikerer at en økende infestasjonsgrad reduserer sannsynligheten for at en ørret returnerer. Denne masteravhandlingen viser at denne typer studier kan være nyttig for å definere grenseverdier for når sjøørret ikke kommer tilbake fra sjøvandringen basert på luseinfestasjoner. Men det er imidlertid et behov for å repetere denne typen studier både over år og for ulike bestander. Majoriteten av fisken returnerte ved vanntemperaturer på 11 - 14 ºC i estuariet, antagelig som en avveining mellom optimal veksttemperatur og energiforbruk eller på grunn av en sesongeffekt. Majoriteten av ørreten valgte å returnere ved høyt tidevann fra sjø til elv, da dette trolig reduserer tilgjengeligheten for terrestriske rovdyr og gir større vannmasser for ørreten etter hvert som den vandrer opp elven. Denne masteravhandlingen viser at abiotiske forhold i estuariet trolig kan regulere når sjå ørret returnerer fra det marine miljø til ferskvann, og dermed bidrar med ny innsikt for fremtidige studier som ønsker å besvare spørsmål relatert til migrasjonsatferden til retur sjøørret.

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1 INTRODUCTION

The aquaculture industry has had a prominent growth in Norway for the past decades. More than 1.3 billion tons of farmed Atlantic salmon (*Salmo salar*) was produced in 2019 (SSB, 2020). Advancements in technology as well as a better biological understanding of producing marine organisms has enabled such a development. However, an increasing production of salmon provides the marine parasite, sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*), a continuous supply of hosts throughout the year (Grefsrud et al. 2020). As a result, the overall lice-infestation pressure within wild salmonids stocks of Atlantic salmon, sea trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) increases (Finstad et al., 2021). Like other crustaceans, the sea lice have multiple life stages. The number of life stages varies among the different species of sea lice. *Lepeophtheirus salmonis* starts its life cycle as a planktonic nauplii larvae until it develops in to the copepodite stage. This is when the sea lice become infectious and latch on to the host. In the next life stage, it will then start to feed off the hosts skin and mucus in a stationary position. The final stages in the life cycle are the preadult and adult stages, where the lice become mobile and able to reposition itself on the hosts body (Dalvin, 2018).

The brown trout has a complex life cycle where some will spawn and reside in freshwater for their entire life. Others will spawn in freshwater, then become anadromous and perform a marine migration with the intention of enhancing growth, fitness and fecundity as the marine environment offers a larger quantity of nutritious prey items compared to the freshwater system (Thorstad et al., 2016). A marine migration also entails a considerable risk of predation and infestations of sea lice as well as an energy cost related to the migration distance (Thorstad et al., 2016). Sea trout rarely travel more than 80 km away from their respective river during their marine migration (Thorstad et al., 2016). A recent study of migrating trout post-smolt conducted in the fjord system of Alta, found the trout post-smolts to reside within 18 km of the fjord during the entire marine growth phase (Atencio et al., 2021). Migrating sea trout will consequently reside in coastal waters with a high lice-infestation pressure for extended periods. The effects of a sea lice infestation may therefore be considerable within populations of this salmonid species. Sea trout has been observed to alter their migration behavior by prematurely returning to freshwater or areas with lower salinity to mitigate the effect of the lice (Halttunen et al., 2018), as the sea lice does not tolerate low salinities for extended periods (Wright et al. 2016). Although sea trout avoids direct mortality in a short-term perspective, this strategy compromise the duration of the marine growth period. Consequently, the fecundity along with the spawning success could be reduced (Nevoux et al., 2019).

Laboratory and field studies suggests that sea lice infestations may have lethal effects on wild salmonids due to an osmoregulatory dysfunction or tissue damage which could lead to a secondary infection of bacteria or viruses. The risk of being caught by predators may also increase due to the fish's weakened state in the natural environment (Thorstad et al., 2015). The suggested mortality threshold of lice for sea trout varies among studies. An expected mortality or compromised reproduction for sea trout due to 50 mobile lice was suggested in Bjørn & Finstad, (1997) and Taranger et al., (2012). As little as 13 mobile lice or a mass specific intensity of approximately 0.35 lice g^{-1} were likely to cause physiological stress in sea trout from 19-70g (Wells et al., 2006; 2007). Tveiten et al., (2010), expected a threshold a 100 % mortality rate of >0.15 lice g^{-1} for mature specimen of Arctic charr, while Tveiten et al., (2010), observed osmoregulatory failure and acute mortality at 0.1 lice g^{-1}. Elevated infestation rates of 0.5-2.1 lice g^{-1}

caused osmoregulatory breakdown in wild sea trout and artic charr in areas close to salmon farms (Bjørn et al., 2001). Wells et al., (2006; 2007), measured the influence of various life stages of lice on the health status of anadromous sea trout. Their findings indicate that the mobile stages of lice pose a greater threat to the trout and are more likely to cause harmful physiological effects than immobile stages. It is worth mentioning that these thresholds are based on laboratory trials and does not necessary reflect the natural conditions in the wild. The effect of the lice can be magnified by suboptimal conditions such as poor water quality (Finstad et al., 2007). Infestation levels below lethal values might also result in changes in the behavior of the fish.

Although trout has been observed to return prematurely as a response to an elevated sea lice infestation pressure, other factors also affect the timing of the habitat shift. As sea trout are poikilothermic, their metabolism and metabolic processes increase or decrease according to the temperature of their surroundings. A study conducted in Danish rivers (Kristensen et al., 2018), found that temperature ranges of 10.4-13 ºC were preferred by adult trout ascending the rivers in the autumn. When temperatures rose above 17 ºC, the trout would seek to colder water masses and reside at 5-20m depth for days (Kristensen et al., 2018). Another study conducted in the Norwegian river, Imsa, from 1976 to 1999 found that an increasing water flow up to 8.75 $m^3 s^{-1}$ positively influenced the likelihood of a trout ascending. Waters flow above this threshold seemed to decrease the upstream migration as it became too energy demanding to swim against the stronger currents (Jonsson & Jonsson, 2002). Whilst these studies provide some evidence for various factors influencing the habitat choice, to the best of mye knowledge, none have thoroughly studied this effect. The influence of the tide as well as the dial light situation on the timing of the return from sea to freshwater are still poorly understood. In 2017, a Norwegian expert group of leading scientists was appointed by Nærings- og fiskeridepartementet (NFD) to evaluate the effect of sea lice on wild salmonids produced by the salmon farming (Vollset et al., 2018). In 2019, they concluded that knowledge regarding the sea trout's migration behavior and habitat choice during a sea lice infestation are lacking (Nilsen et al., 2019).

The aim of this master thesis was to investigate if various morphometric traits and the degree of sea lice infestations would impact the likelihood of a returning to freshwater by examining trout caught in the sea at Agdenes outside the Norwegian river, Fremstadvassdraget, Trøndelag, from June till October. It was also investigated if an increasing number of sea lice would significantly affect the date for when the migrating trout returned to the river. Finally, it was examined if given light conditions, specific tidal- or temperature ranges or a specific water flow would influence the timing of migrating from the sea to the river at the end of the marine growth phase. These findings will aid in the planning of local management strategies and contribute to fill knowledge gaps related to the implementation of sea trout as an indicator species in the national aquaculture management system (Trafikklysstemet).

1.1 Hypothesis

1. An increasing sea lice infestation will reduce the likelihood of sea trout returning from their marine growth phase due to detrimental physiological effects and an increased risk of mortality at sea.
2. An increasing sea lice infestation will increase the likelihood of sea trout to return to freshwater earlier as sea lice are unable to tolerate low salinities for extended periods.
3. Timing of migration from the sea to freshwater is regulated by abiotic conditions, in order to reduce predation risk and increase accessibility to the river.

2 MATERIALS AND METHODS

2.1 The sampling site

The river of Heggaelva lies in the municipality of Agdenes and drains into Vassbygda in Trondheimfjorden. The river is a part of the complex watercourse named Fremstadvassdraget. The lake of Litlevatnet is connected to Storvatnet by a tributary. The outlet of Litlvatnet is the uppermost part of the river Heggaelva. The length of the river Heggaelva is approximately 1 km and it drops 5 m from Litlvatnet to the outlet to the sea (Fossheim, 2015). The predominant species of fish in the watercourse are brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) which utilizes parts of the river as spawning grounds. From Storvatnet, the residing salmonids can choose to migrate up into Musdalselva or Vollaelva. Specimen of the European flounder (*Platichthys flesus*) and the European eel (*Anguilla Anguilla*) have been observed in the water course as well (Ulsund, 2013; Fossheim, 2015).

In 1983, Litlvatnet was protected as a nature reserve to preserve one of a few eutrophic lakes in the county Trøndelag. Since then, the condition of the lake has deteriorated due to an overload of nutrients from nearby agriculture causing an overgrowth of the vegetation surrounding the water course. The water level in Litlvatnet has been adjusted several times since the 1960s. Mainly by excavating the outlet stream, leaving the uppermost part of the river Heggaelva unsuitable for spawning. In 1993, the water was elevated to the same level as when the lake was preserved by constructing a threshold in the outlet stream (Winnem, 2010).

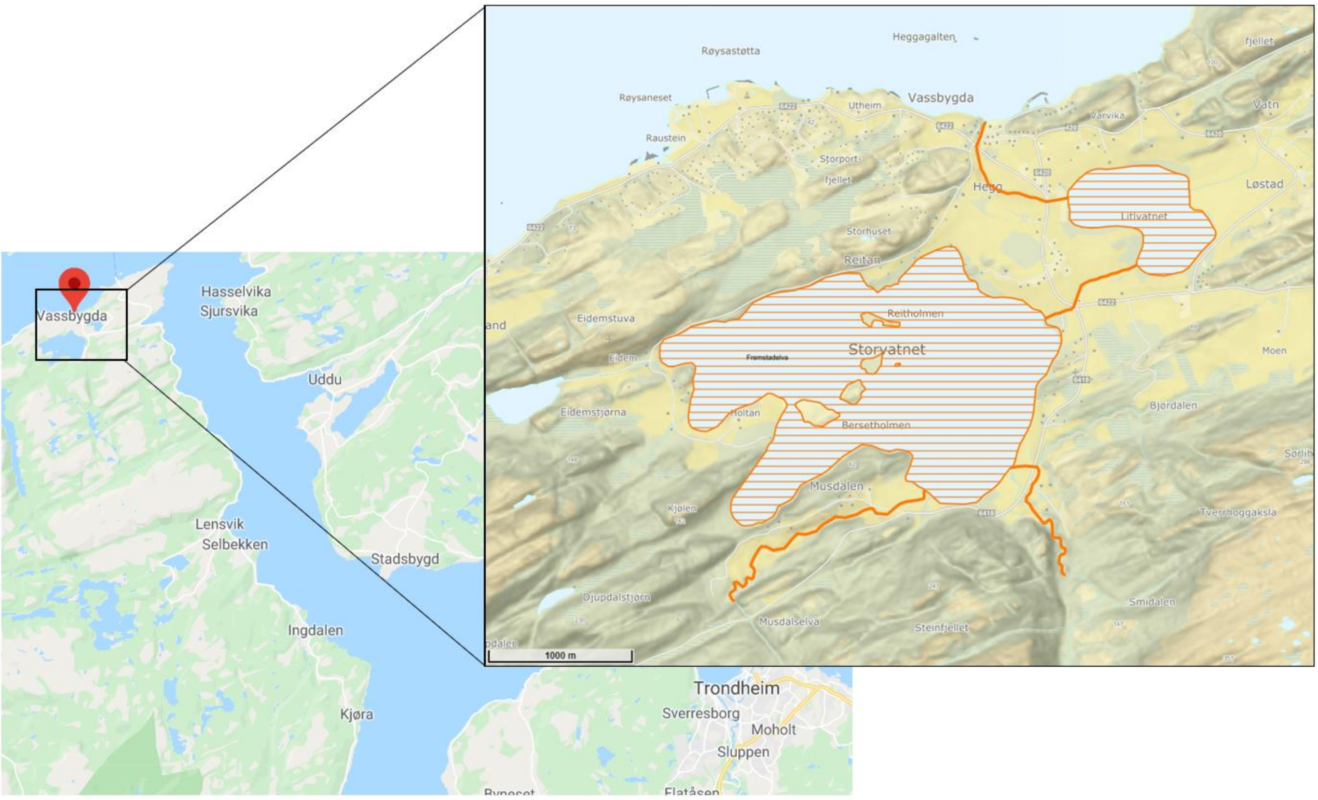
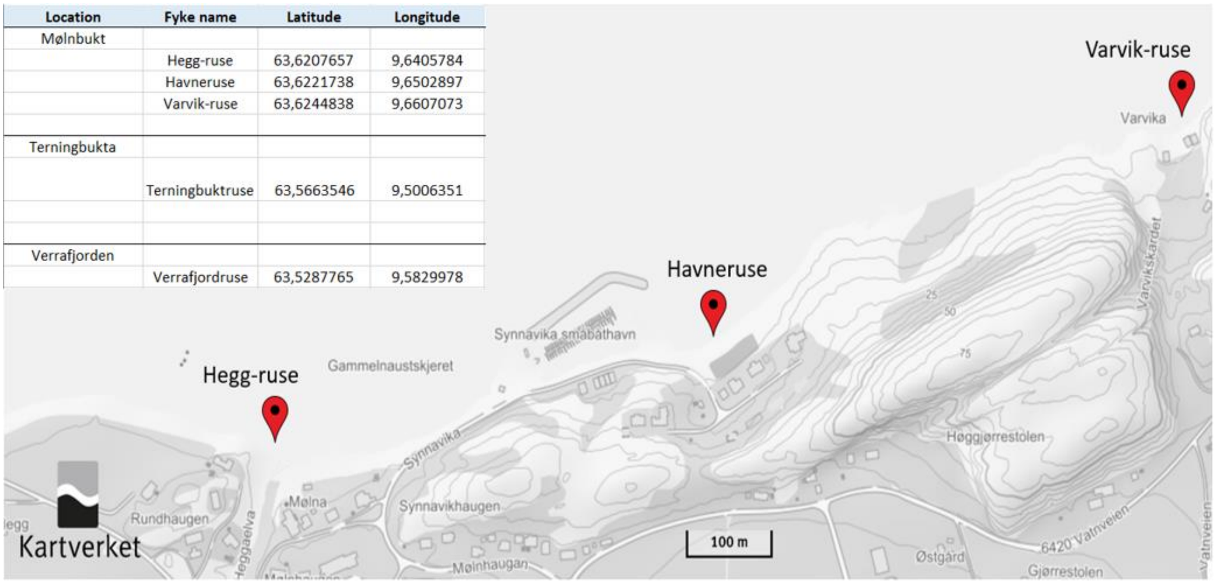


Figure 1: The shaded areas and the orange lines show the anadromous parts of Fremstadvassdraged including the tributaries to Storvatnet (Miljødirektoratet, 2013).

2.2 Sampling wild sea trout

The sampling of sea trout started on the 1st of June and lasted until the 10th of July 2020. The trout were sampled using three fyke-nets installed in the bays outside- as well as to the north of the river, Heggaelva (Figure 2). The fyke-net named Hegg-ruse, would remain outside the river mouth of Hegga with the purpose of catching the trout migration from the river Heggaelva. Havneruse and Varvik-ruse would be relocated in periods with low catches to optimize the sampling.



Location	Fyke name	Latitude	Longitude
Mølnbukt			
	Hegg-ruse	63,6207657	9,6405784
	Havneruse	63,6221738	9,6502897
	Varvik-ruse	63,6244838	9,6607073
Terningbukta			
	Terningbuktruse	63,5663546	9,5006351
Verrafjorden			
	Verrafjordruse	63,5287765	9,5829978

Figure 2: The locations and coordinates of the fyke nets. Photo: Kartverket

The opening of the fyke-nets measured 5 m width and 3.5 m tall with a wingspan of 15 m. The leading measured 25 m from the wedge of the fyke-net to the end (Appendix 1). The end of the leading net was anchored at the top of the sub littoral zone (Figure 3). This reduced the likelihood of trout avoiding the leading net by blocking the gap between the leading net and the water's edge. The catch chambers of the fyke-nets were manually emptied once a day (twice if the water temperature was high and/or if the catch was large). This procedure was carried out by untying the knot at the end of the catching chamber and stretching out the opening (Figure 4). Thereafter the fish was gently moved from the chamber over to a black 60 l bucket with sea water for storing during the procedure described in part 2.3. The days where the air temperature exceeded 20 °C, the fish was stored in tube-shaped sea cages (diameter = 1 m, Length = 1.5 m, mesh size = 2 cm) kept in the sea instead of bucket to prevent overheating. These cages would also be used when the catches exceeded 15 fish per fyke-net.

Figure 3: The compartments and the setup of the fyke nets. Photo: Nicolas Sperre

Figure 4: An underwater photo of the fyke net's catching chamber during an emptying procedure. Photo: Johanna, Järnegren

2.3 PIT-tagging, lice counting and morphometric parameters

An air-pump was used to maintain a sufficient level of oxygen in the water in the bucket where the fish was kept from capture to tagging. The top of the bucket was covered to prevent fish from jumping out and to provide shade to reduce stress. To prevent the movement of the boat interfering with the analyses, the boat was docked during tagging and measurements. Each trout was collected from the holding container using a knotless handheld net and transferred to a 10-l bucket containing an anesthetic solution composed AQUI-S and seawater. The concentration used was 10-14 mg isoeugenol which corresponds to 1.9 – 2.6 ml/100 l of sea water. The anesthetic was diluted according to recommendations by Legemiddelindustrien (LMI) (Legemiddelindustrien, 2019). Each trout was kept under anesthesia for approximately one minute. However, visual ques such as gill frequency and the tail root pinch reflex were monitored to determine if the fish was sufficiently anesthetized. As the efficiency of the anesthesia increase with water temperature, the holding time would vary (Legemiddelindustrien, 2019).

When the trout was deemed sufficiently anesthetized it was handed over for identification marking. All handling of the trout above water was carried out using latex gloves to reduce the impacts on the condition of the skin and avoid direct contact with the anesthetic. To check if the fish was already tagged and prevent the trout from being tagged twice, a handheld PIT-reader of the model Biomark HPR lite was used (Biomark). If a PIT-tag was detected, the identification number was recorded, and the fish was passed on for the morphometric analyzes. If no tag was detected, a PIT-tag was injected in the true left side of the fish's abdomen (Figure 5). The PIT-tags used for this study was Biomark's model, APT12 (Biomark). These tags are pre-loaded within a needle which requires Biomark's MK25 PIT-gun for injections (Biomark). Following the injection, the fish was scanned, and the identification number was recorded. The personnel tagging the fish were required to have undergone the proper training and have passed NINA's course in Laboratory Animal Science. These requirements would secure good animal welfare and prohibit the introduction of observer effects causing imprecision in the tagging . All handling and tagging were approved by Mattilsynet. Fish >8.5 cm was tagged.

Figure 5: The PIT-tagging procedure accompanied by a picture of the PIT-reader and the weight used in this study. Photo: Nicolas Sperre

The total body- and fork length were measured using a designated measuring tube (Figure 6). A container filled with water was placed on top of a digital weight of the brand, Kern, while measuring the mass of the fish. Total body length and the body mass were used to calculate the Fulton's condition factor K for each individual according to this formula: $K = 100\ W(g) * L(cm)^{-3}$ (Ricker, 1975).

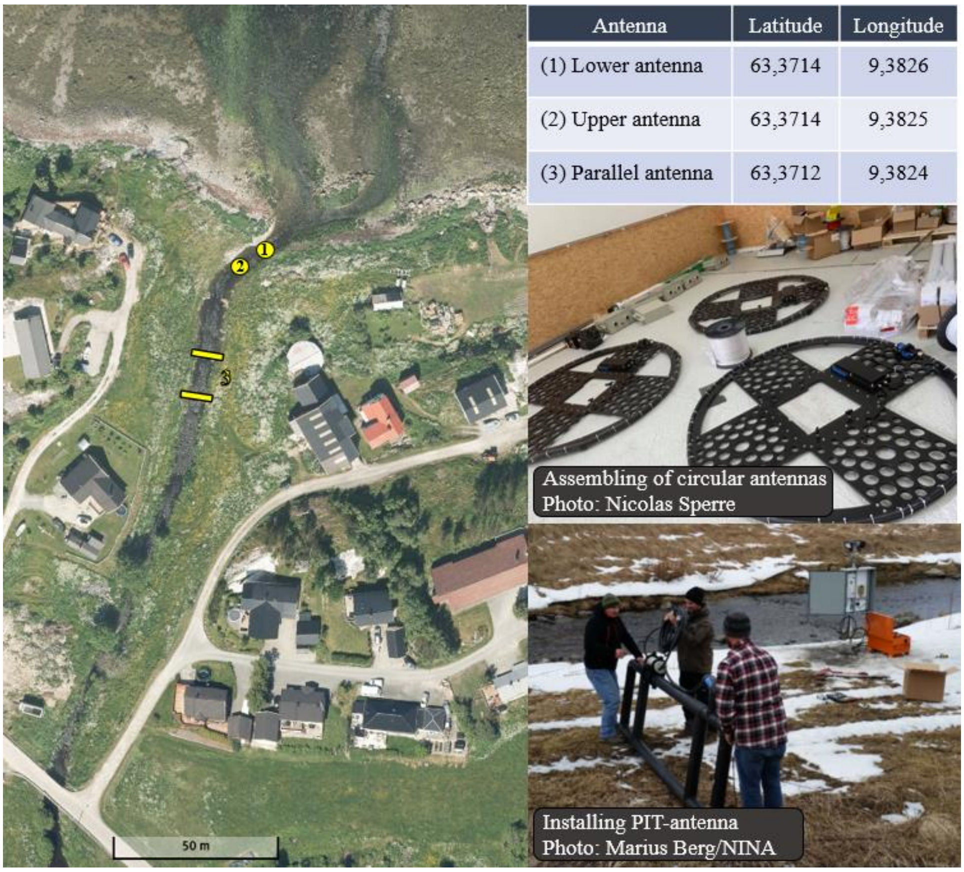
Lice was manually counted in a white rectangular tray, which would act as a contrasting background to the color of the sea lice. A headlamp was worn by the lice counter to optimize the visibility of the lice (Figure 7). This procedure was exclusively carried out by personnel certified to count lice as a measure to reduce the likelihood of introducing deviations in the results. When all analyses were conducted, the fish was placed in a tube-shaped cage outside the gunwale of the boat for recovery. The recovery time was less than 15 minutes.

Figure 6: The measuring tube and procedure. Photo: Astrid Tonstad

Figure 7: The lice counting procedure and an identification key for sea lice by Pharmaq (Pharmaq). Photo: Nicolas Sperre

2.4 Surveillance of the migration pattern

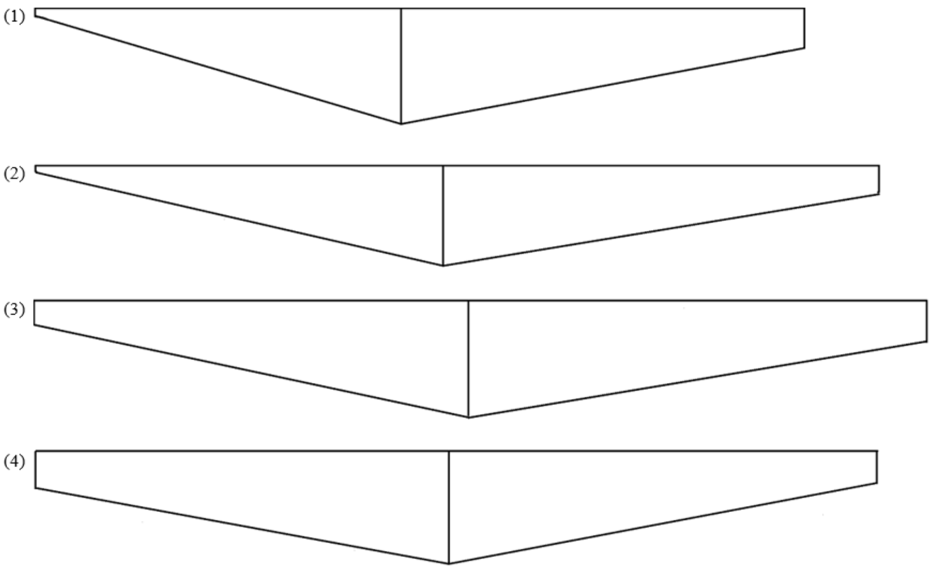
The surveillance-setup was composed of two parallel PIT-antennas and two Biomark circular PIT-antennas (Berntsen et al., 2019; Biomark) (Figure 8). The circular PIT-antennas were installed in the narrowest part of the river above the rapid which leads into the estuary (Figure 9). This would leave the PIT-tagged trout with a minimal of amount of area to slip past the antenna and remain undetected on its way up the river. The antenna diameter of 1.8 m provided a sufficient coverage of the river. Stones were stacked on either side of the antennas with the purpose of anchoring and guiding fish over the scanning-zone of the antennas (Figures 9-10).



Antenna	Latitude	Longitude
(1) Lower antenna	63,3714	9,3826
(2) Upper antenna	63,3714	9,3825
(3) Parallel antenna	63,3712	9,3824

Figure 8: The locations for the PIT-antennas as well as depictions. Map: norgeskart.no

Figure 9: The setup for the upper- and lower circular antennas. Photo: Nicolas Sperre



Location	Width (cm)	Depth true-left (cm)	Depth middle (cm)	Depth true-right (cm)
(1) Lower antenna	425	5	62	22
(2) Upper antenna	580	3	51	10
(3) Lower parallel-antenna	710	10	75	17
(4) Upper parallel- antenna	590	22	75	20

Figure 10: The profile of stream in addition to the dimensions of the cross sections.

The water temperature and the salinity were monitored at various locations in the water course as well as outside the river outlet throughout the field period by using data storage tags (Star-Oddi). These tags were placed in protective capsules anchored to bottom in the middle of the river by a 5 kg chain link (Figure 11). Sensor number six was tied to a buoy via a 50 cm rope to monitor the upper layer of water during the season. The surveillance of the migration pattern of the trout in the river of Hegga lasted from the 1st of June until the 30th of September. On the 30th of September, the circular antennas were retrieved from the river and the logging history from each of the antennas were downloaded. The software used for this procedure was Biomark Tag Manager. The data from the stationary antenna was retrieved online.

Location	DST.-sensor ID#
1	6958
2	6960
3	6946
4	6947
5 (bottom)	6959
6 (top)	5459

Figure 11: The locations for the sensors. Map: norgeskart.no

2.5 Analysis and handling of data

In some cases, tagged and examined trout were recaptured in the fyke net and analyzed for a second time at sea, resulting in two registrations of the same fish in the dataset. In those cases, the second registration was manually filtered out of the dataset to ensure standardized conditions for all sampled fish.

The swimming path of each individual fish was interpreted by looking at registrations from each of the four antennas in relation to each other. By inserting the timestamp for when the trout would swim past each antenna, it would indicate if the fish were headed up or down the river at the given date (Appendix 1). The direction the fish was heading at the last registration would determine if the fish had been temporarily residing in the river or returning permanently for the season. A singular registration on a single antenna which was not accompanied by correlated detections on another antenna was interpreted as a false detection. Such detections could be caused by nearby radio transmitting devices or ferrous metals interfering with the electromagnetic communication. False detections were filtered out before further analysis. Each sampled trout was classified as either not returned, returned or uncertain based on this evaluation.

The estimated tide at Agdenes for when each returning trout completed their earliest registered return was added to the dataset using historical data from the database of Kartverket as it provides hourly estimates of the tide at a given location (Kartverket, 2020). As the registrations for the return were fractured into hour and minutes, the timestamp was rounded to the nearest whole hour. The combined precipitation for the last return date and the previous day was added as a predictor variable to access the effect of the waterflow. The meteorological data was retried from a weather station located at Ørland Airport, 8.85 km North of Hegga (Klimaservicesenter, 2020).

2.6 Statistical analyzes

Factors influencing returning trout

A GLM (Generalized linear model) was used to investigate hypothesis 1 which states that an increasing number of sea lice will reduce the likelihood of a sea trout returning at end of the marine growth phase due to a reduced fitness level. RStudio version 1.3.1093 was used for this analysis (RStudio, 2021). This model was selected as it is able to handle non-normal distributed data when comparing the influence of each predictor variables. Whether a trout would return or not was set as the binary response variable. The total body length, the condition factor and the total number of lice were set as predictor variables. The link was set to logit and family set to binomial. To avoid autocorrelation between the total body length (L) and the condition factor (K) when applying both predictors in the same model, the residual values from the linear model $\log(K) \sim \log(L)$ was used to represent the K-factor values. The predictor variables were scaled and centered in order to yield an equal scale of value when comparing effect sizes between them, by using the "scale" function in RStudio. The variance inflation factor (VIF) was calculated using the R package, "performance", to analyze the magnitude of multicollinearity between the predictors (Documentation, 2020). The figures used to present the results for this statistical analysis were made by using the R package ggplot2 (Wickham, 2016).

A Wilcoxon signed-rank sum (Mann–Whitney U) test was used to further investigate the relationship between the return rate and the number of lice per unit of mass (lice g^{-1}). This allows for a statistical evaluation of the influence of lice where the bodyweight of the fish is considered. The null hypothesis tested was that the median mass specific intensity (lice g^{-1}) of the returning trout equals that of the non-returning trout. This test was selected as it allows for non-normal distributions within the sample groups (RStudio, 2021).

The infestation pressure affecting the date of return

To investigate how the period between the lice counting and the return date was affected by various measures of sea lice infestation, a continuous variable for the duration of the period was constructed by using the Julian date (# of days since the 1st of January 2020 plus the # of hours into the following day divided by 24) between the lice-counting day and the day the trout returned. The time interval was correlated with each of the three predictor variables for the number of sea lice (immobile lice, mobile lice, and lice total), as well as the number of lice per gram body weight as a predictor in a regression analysis to investigate hypothesis 2. To test how the number of lice affected the return date regardless of when the lice counting was carried out, the same analysis was applied by correlating the Julian date with each of the four predictor variables for the number of sea lice. Both analyses were conducted using RStudio.

Factors affecting the migration pattern

Finally, it was investigated if the following four abiotic variables influenced the timing for when the trout started their migration from the sea to the river: Tides, precipitation, light conditions, and the water temperature in the estuary. All variables were investigated by using a Fisher's Exact Test in RStudio. Since the observational data consisted of small numbers, and in some cases less than five, the Fisher's Exact Test was chosen over a standard Chi-squared Test. The null hypotheses tested states that there is no significant variance between the expected distribution and observed distribution of returning trout.

To test if higher water levels increase the likelihood of a trout deciding to return, three categories of tidal ranges were used (0 – 100 cm, 101 – 200 cm, and 201 – 300 cm). This represents the first column in the contingency table. The second column contained the distributed number of fish given that the fish returned at random tides, estimated from the distribution of hours the tide would fall within each of the three categories throughout the period. The third column contained the number of fish that returned within each of three tide categories (Appendix 1).

The same procedure was used to investigate the influence of the precipitation. The first column contained four categories of precipitation ranges measured in the field period (0 – 10 mm, 10.1 mm – 20 mm, 20.1 – 30 mm and 30.1 – 40 mm). The second column contained the distributed number of fish given that the fish returned at random precipitation intervals, estimated from the distribution of days the precipitation for the last 48 hours would fall within each of the four categories throughout the period. The third column contained the number of fish that returned within each of the four precipitation categories (Appendix 1).

To investigate the influence of the light conditions throughout the day, the 24-hour span of a day was divided into 4 categories (00:01 – 06:00, 06:0 – 12:00, 12.01 – 18:00 and 18:01 – 24:00) in the first column. Each cell in the second column contained equal values of 25 % of the fish, as each time interval would occur once a day. The third column contained the number of fish that returned within each of the four time categories (Appendix 1).

The first column in the contingency table for the influence of water temperature were composed of three temperature intervals (8 – 11 ºC, 11.01 – 14 ºC and 14.01 – 17 ºC). The second column contained the distributed number of fish given that the fish returned at random temperature intervals, estimated from the distribution of hours in the return period where the water temperature in the estuary outside the river Heggaelva would fall within each interval. The third column contained the number of fish that returned within each of the three intervals (Appendix 1).

3 RESULTS

In total, 191 sea trout were sampled at Agdenes during the six-week field period. The first two weeks were characterized by low catches. By the third week the catches nearly tripled and remained consistently high until the last week. 63 of the sampled trout (33 %) returned at the end of the marine growth phase while 128 did not. The mass-specific lice intensity followed a bell-shaped pattern throughout the period with an average peek intensity of 0.41 lice g^{-1} in week 26 (Table 7). The lice intensity peeked in week 28 with an average peek intensity of 52.9 lice fish-1 (Table 7). The number of newly hatched nauplii larvae reported from nearby salmon farms increased exponentially during the same week (Mattilsynet, 2020). 9.5 % of the returning and 32.8 % of the non-returning trout had a mass specific lice intensity of ≥ 0.3 lice g^{-1}, while 33.3 % of the returning trout and 52.3 % of the non-returning trout had a mass specific lice intensity of ≥ 0.2 lice g^{-1} (Table 8). None of the returning trout had more than 0.45 lice g^{-1}, while 32 (25 %) of the non-returning trout had a mass specific lice intensity above 0.45 lice g^{-1} (Figure 12).

Table 7: The examination material used in this study given as the week number, number of fish (n), mass, total length, condition factor, lice intensity, and lice mass-specific intensity of the sampled trout with standard deviation.

Week	n	Mass (g) ± SD	Total length (mm) ± SD	Condition factor ± SD	Intensity (lice $fish^{-1}$) ± SD	Mass-specific intensity (lice g^{-1}) ± SD
23	7	232 ± 179.9	288 ± 85	0.806 ± 0.038	16.6 ± 8	0.12 ± 0.09
24	19	130 ± 88.3	240 ± 68.9	0.812 ± 0.059	36.7 ± 47.9	0.20 ± 0.17
25	64	215 ± 177.3	280 ± 60	0.812 ± 0.099	47.4 ± 32.6	0.32 ± 0.29
26	46	255 ± 319.5	277 ± 155.5	0.851 ± 0.101	45.7 ± 29.8	0.41 ± 0.43
27	48	424 ± 398.2	331 ± 93.3	0.888 ± 0.091	39.1 ± 18.9	0.20 ± 0.22
28	7	1018 ± 760	428 ± 114.6	1.010 ± 0.164	52.9 ± 45	0.11 ± 0.11

Table 8: Mass-specific intensity intervals (total number of lice including all life stages) accompanied by the corresponding percentages of returning and non-returning trout within the intervals.

Mass-specific intensity (lice g^{-1})	Percentage of returning trout	Percentage of non-returning trout
≥ 0.2	33.3	52.3
≥ 0.3	9.5	32.8
≥ 0.5	0	22.8

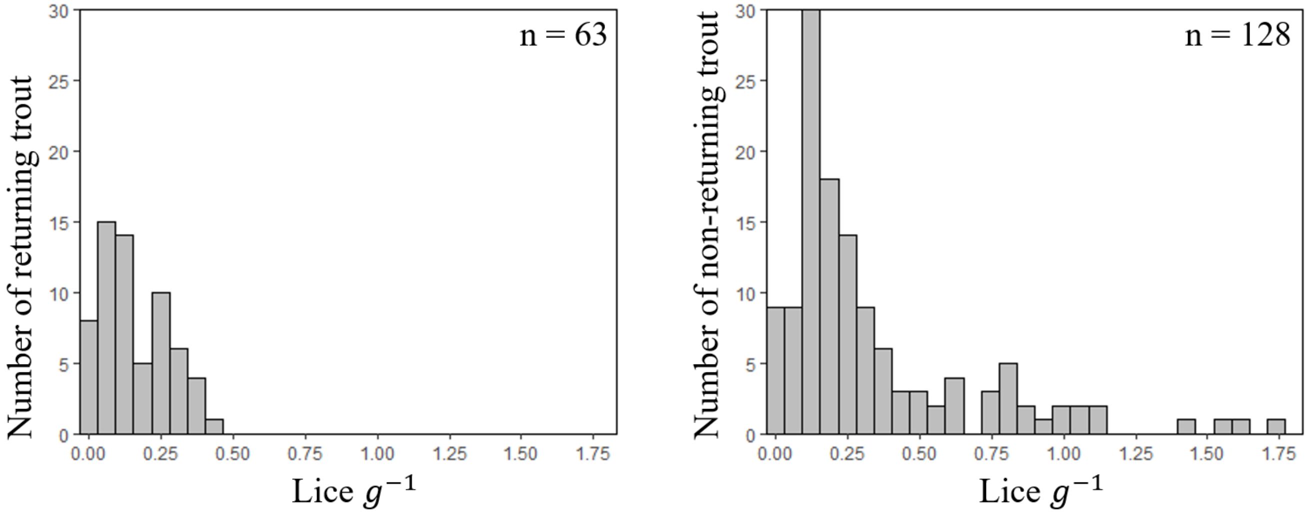


Figure 12: Histograms of the lice distributions (total number of lice including all life stages) on the returning and non-returning trout with the number of trout on the y-axis and lice g[-1] on the x-axis.

3.1 The influence of a lice infestation on returning trout

The GLM yielded an AIC score of 227.3 with a null deviance of 242.2 with 190 d.f. (degrees of freedom). Every predictor had a VIF-score below 1.2, indicating a low degree of multicollinearity. The likelihood of return was found to be positively influenced by the total length of the trout ($p < 0.001$), indicating that an increasing body length increase the likelihood of a trout returning. The total number of sea lice as well as the trout's condition factor was found to have no significant association to the likelihood of a return (p lice = 0.23, p condition factor = 0.43) (Appendix 2).

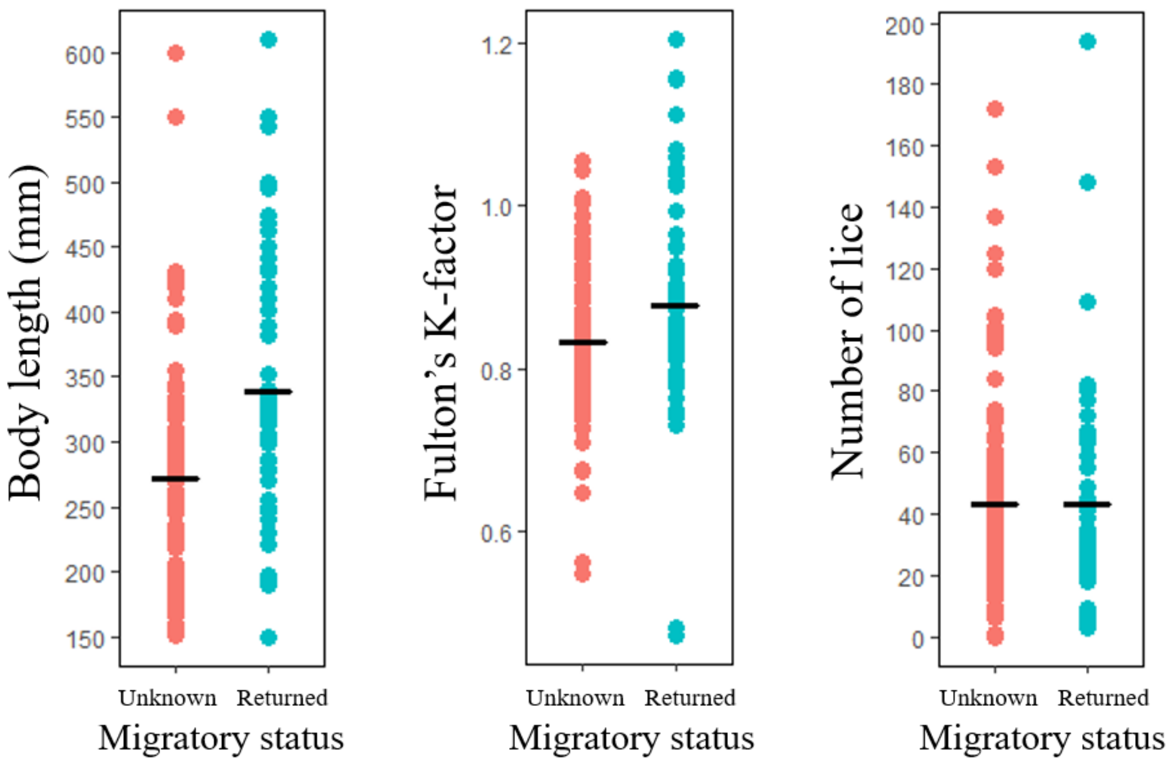


Figure 13: The three predictor variables from the GLM-analysis on the y-axis and the migratory status of the given trout on the x-axis including the mean represented as a horizontal black crossbar.

The Wilcoxon signed-rank sum test yielded W-value of 5458 with a confidence interval between 0.13 and 0.43, suggesting that is likely that the median of lice g^{-1} for the population at Agdenes lies within this interval. The median mass specific intensity of the non-returning trout was found to significantly larger than that of the returning trout ($p < 0.001$) (Figure 14).

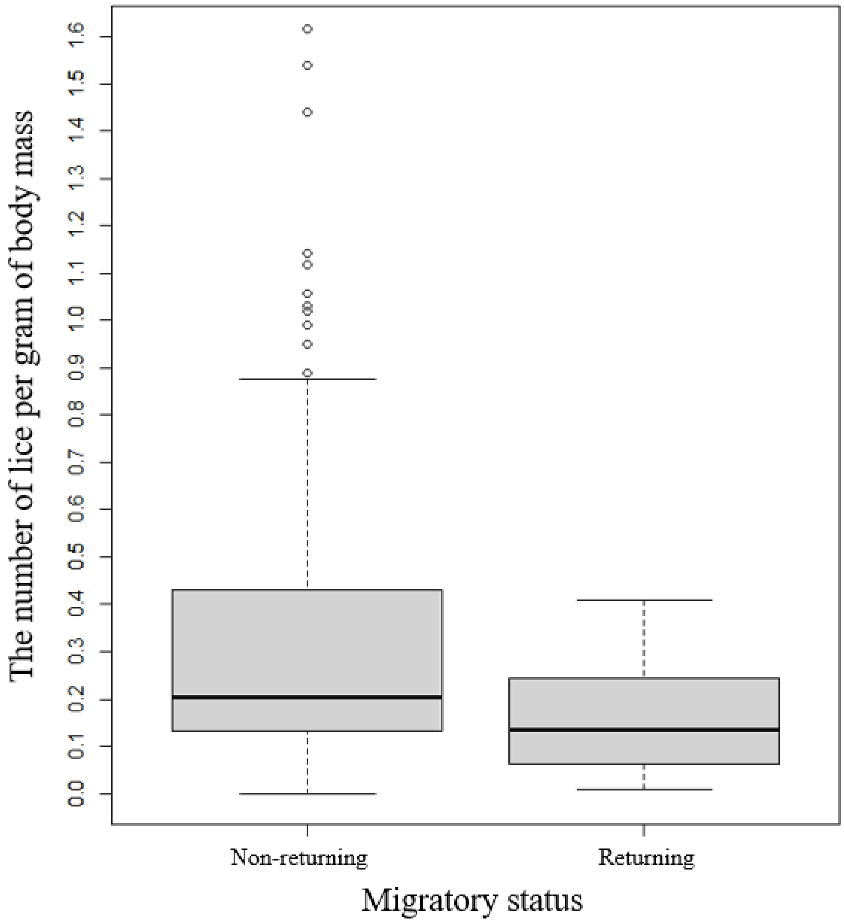


Figure 14: Boxplot of the median mass specific intensities of the non-returning and the returning trout including. The migratory status is described on the x-axis and the number of lice per gram of body mass (lice g^{-1}) is described on the y-axis.

3.2 Infestation pressure in relation duration of the marine phase

The number of sea lice regardless of the life stage as well as the mass specific intensity had no significant influence on the return date or the duration of the period between the lice counting day and the day of return (Table 10) (Figure 15). However, there was a nonsignificant trend indicating that the number of attached immobile lice positively related to the period ($p = 0.7$). Although this may indicate a trend, only 5 % of the variation is accounted for in the regression (R-squared = 0.053). There was no influence by the number of sea lice of any life stage or the number of lice g^{-1} on the date of return (Table 11) (Figure 16).

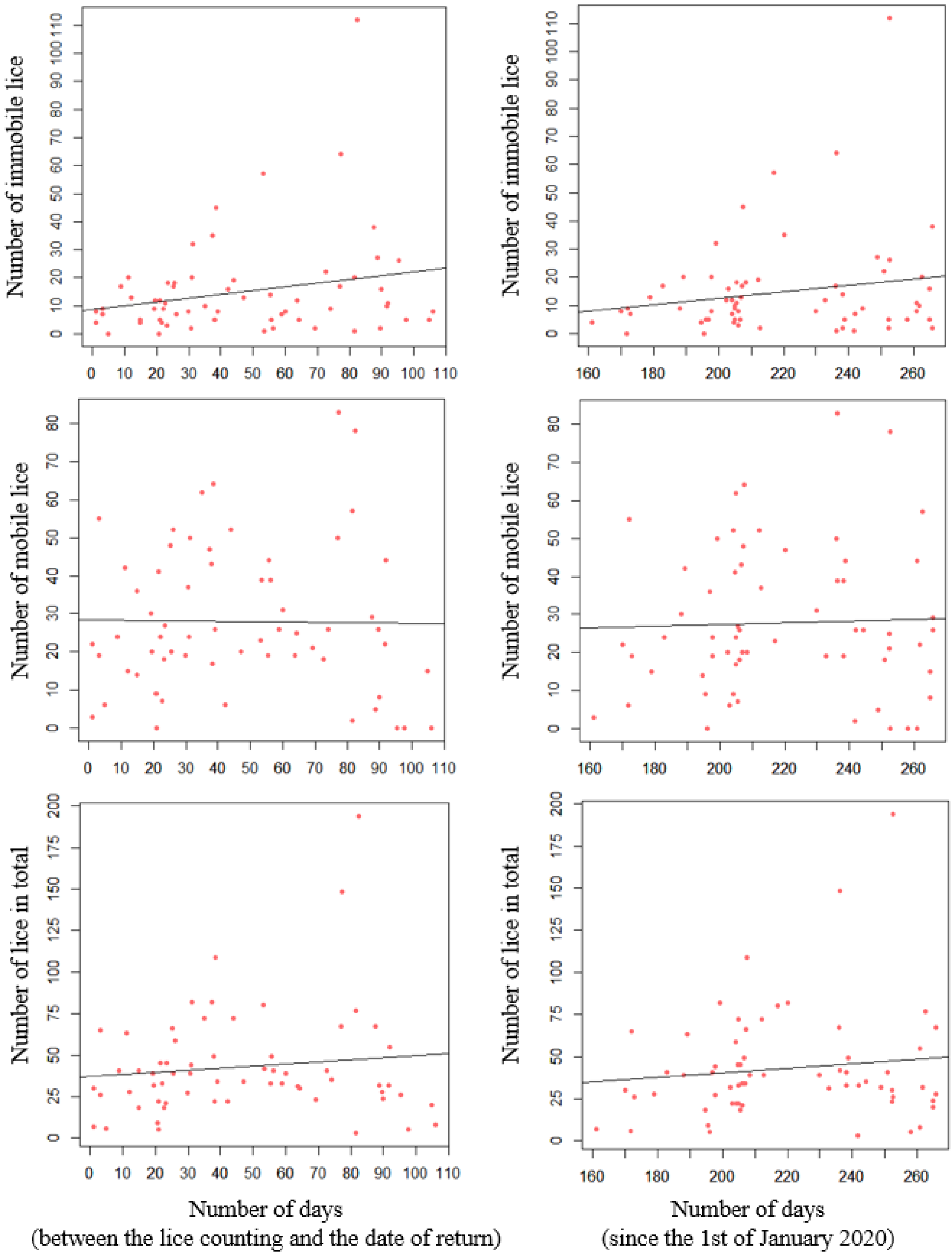


Figure 15: Linear regressions of the period between the lice counting and the date of return in the left column accompanied by the linear regressions of the date of return in the right column. The number of days on x-axis and the number of various life stages of sea lice on the y-axis.

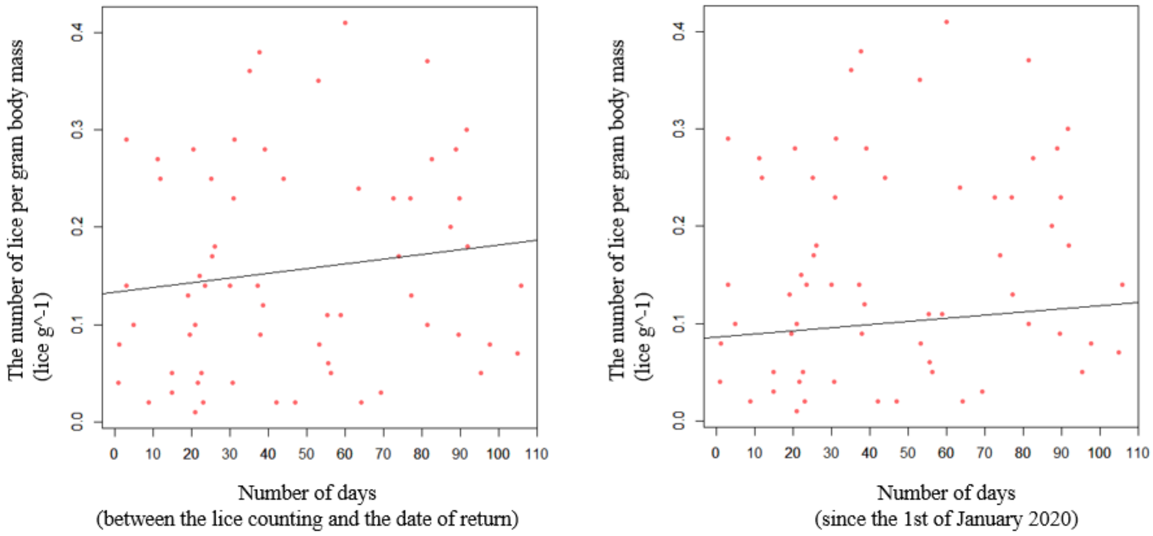


Figure 16: Linear regressions of the period between the lice counting and the date of return to the left accompanied by the linear regressions of the date of return to the right. The number of days on x-axis and the total number of lice (all life stages included) per gram of body mass (lice g^{-1}) on the y-axis.

Table 10: Linear regressions of the period between the lice counting and the return date with the number of lice as the dependent variable accompanied by the estimated R-squared and P-values.

Lice life stage	Regression	R-squared	p
Immobile lice	y = 8.59 + 0.14x	0.0527	0.070
Mobile lice	y = 28.28 – 0.01x	0.0002	0.919
Lice total	y = 37.07 + 0.14x	0.0142	0.352
Lice g^{-1}	y = 0.13 + 0.0005x	0.0186	0.287

Table 11: Linear regressions of the date of return with the number of lice as the dependent variable accompanied by the estimated R-squared and P-values.

Lice life stage	Regression	R-squared	p
Immobile lice	y = –10.18 + 0.11x	0.0341	0.556
Mobile lice	y = 23.10 + 0.02x	0.0011	0.227
Lice total	y = 12.88 + 0.14x	0.0149	0.685
Lice g^{-1}	y = 0.08 + 0.0003x	0.0071	0.511

3.3 Abiotic preferences among returning trout

Among the returning trout, higher tidal ranges of 201 – 300 cm were preferred when initiating their migration upstream. The Fisher's Exact Test showed a statistically significant difference between the expected- and observed frequencies of tidal ranges ($p = 0.003$). A statistically significant Fisher's Exact Test revealed that a higher number of fish entered the at 11 to 14 ºC compared to the other temperature ranges tested ($p < 0.001$). No significant differences between the expected- and observed frequencies of precipitation ($p = 0.539$) or light conditions ($p = 0.173$) were found (Appendix 2).

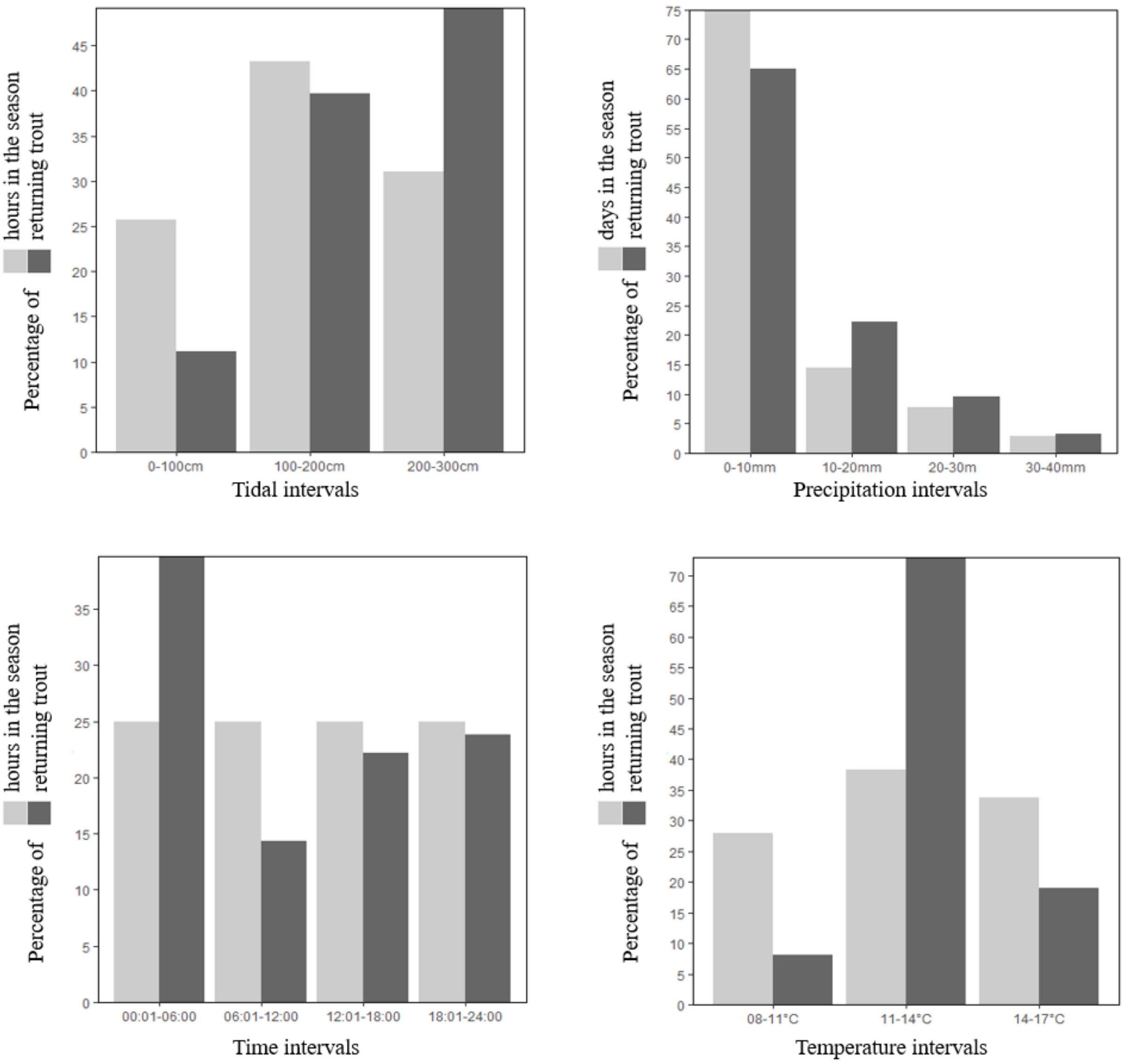


Figure 17: Bar plots of the results from the Fisher's Exact Test with the distribution of intervals on the x-axis and the percentage of returning trout as well as the percentage of the observed distribution of hours/days within the season from the 1st of June until the 30th of September

4 DISCUSSION

4.1 Return of sea trout to the river

The results suggested that an increasing body length increased the likelihood of a trout returning to the river at the end of the marine phase. This interpretation is in accordance with the results from Serra-Llinares et al., (2018), who found higher return rates for larger individuals of trout post-smolts. However, the results contradict the findings of del Villar-Guerra et al., (2019) as individuals classified as parr had higher return rates compared to the smolts and pre-smolts in the Mariager Fjord in Denmark. A size selective predation bias towards larger fish sizes was believed to be the cause. As several studies reviewed in Sogard, (1997), showed a reduced predation risk with an increasing body length, it is uncertain if the findings of del Villar-Guerra et al., (2019) holds true for other populations of anadromous sea trout. Webb et al., (1984) fount that the aerobic efficiency increased in relation to the body length, indicating that the muscle efficiency also increases in relation to body length for rainbow trout (*Oncorhynchus mykiss*). It is uncertain to what degree these characteristics are species dependent. However, the size dependent increase in efficiency was believed to be linked with an increase in surface area of the tail as the fish grows, thus requiring a lower tail-beat amplitude to generate an equal propulsion power. As both species are part of the family of salmonids certain morphological similarities are expected. The body length of brown trout has also been observed to positively correlate with both stamina and burst speed (Ojanguren & Brana, 2003). Eldøy et al., (2021), found larger fish to disperse over greater distances during their marine growth phase as they are less susceptible to predation due to being more powerful swimmers. A faster trout with a greater endurance would be more likely to outswim a predator. Smaller individuals might also pose as an easier prey item increasing the likelihood of predation. The assumption that a larger fish experiences a reduced predation risk is supported by the findings of this thesis suggesting that an increased body length increase likelihood of a return. The average length of the returning trout was also found to be 66.7mm longer than that of the non-returning trout which further supports this assumption. Another explanation is that smaller individuals of trout are more vulnerable to the increasing lice infestation pressure throughout the season. An increasing infestation pressure might force the smaller trout to migrate to the closest freshwater source temporarily or permanently. A severe infestation might also have induced mortality in the smaller individuals. Future studies should consider that the generalizability of the results is limited by the local adaptations to food availability and predation.

A significant difference between the median mass specific intensity of the non-returning trout and the returning trout was found. None of the fish with severe levels of infestations (> 0.45 lice g^{-1}) on the day of lice counting returned to the river. These findings are in consensus with published literature on the topic. Taranger et al., (2015) estimated a 50 % marine mortality for infestation rates of 0.2-0.3 lice g^{-1}, while Taranger et al., (2012), assumed 100 % marine mortality or premature return for juvenile Artic charr < 150g having more than 0.3 lice g^{-1}. As these studies as well as the findings of this thesis suggests, the trout may withstand a low infestation pressure up to a certain threshold until the effects of infestation becomes too detrimental. However, when analyzing the influence of the number of lice on the return rate, no significant influence was found. A possible explanation is that a too low portion of the sampled trout had more than 0.45 lice g^{-1}. Consequently, the GLM might therefore not have been able to detect a significant difference. The finding that none of the fish that had more than 0.45 lice g^{-1} returned support hypothesis 1.

Since the examined trout were gathered from the sea and not from the river itself, the origin of the trout is unknown. Potential strayers from other populations might therefore have been included in the analyses, thus accounting for a portion of the fish not returning. Strayers might also have been carrying a heavier load of lice as they have potentially traveled further through lice infested water masses. Jonsson & Jonsson, (2014), found that larger trout traveled further from their natal river than smaller trout, while Atencio et al., (2021), found that sea trout post-smolts resided within 18 km of their natal fjord system, with 80 % of the detections in this study being registered near the river mouths. As few freshwater systems within an 18 km radius of Agdenes are deemed suitable for hosting major sea trout populations, the likelihood that a large proportion of the examined fish were strayers could be low, although this cannot be ruled out (Appendix 1). Given a random distribution of lice among the fish within this radius, it is unlikely that a small portion of strayers would significantly influence the results.

4.2 The infestation pressure affecting the date of return

A study conducted in Straumsvassdraget, 43.5km northwest of the river Heggaelva, found a reduced marine growth as well as increased Ba:Ca levels for first time migrating smolt with nearby active salmon farms (<14km), indicating a local adaptation to the increased infestation pressure by spending more time in estuaries and freshwater habitats (Eldøy et al., 2020). The study area of Hegga yields similar properties as it lies in close proximity to Straumsvassdraget and has an active salmon farm 12.4km to the west. Nevertheless, a similar behavioral response to the infestation pressure were not found among the trout at Agdenes. One would still expect the heavy infested fish in the dataset to return earlier even though the population have adapted to higher infestations of lice by a reduced marine residence time. Another possible adaptation based on the findings of Eldøy et al., (2020), is that the trout at Agdenes responded quicker to an elevated infestation pressure than compared to populations in areas with a lower infestation pressure throughout the year. Regardless of the adaptations in question, it would be beneficial for the population to reside at sea for as long as possible for optimal growth, granted that the sea lice infestation rates remains below life-threatening levels.

The data in this study only provide information on when the trout leaves the sea and permanently return to the freshwater system of Fremstadvassdraget. This does not necessarily reflect the amount of time the trout spent in low-saline areas to delouse itself. To what extent the fish was temporarily residing in the brackish water zone outside the river is also unknown. This could be considered a confounding factor which weakens the ability to draw conclusions regarding potential premature returns due to lice infestations. Taal et al., (2018), suggested that juvenile trout can alternate between freshwater streams during the marine migration. Hence, the absence of an effect from infestation rates on the return date might also be a result of infested trout prematurely returning to non-natal- or nearby natal streams in the fjord system. In order to examine if this could be the case, additional studies should extend the spatial surveillance of nearby freshwater areas in combination with adjustments allowing for better surveillance of potential trout residing in the estuary. Supplementing this analysis with weekly fyke net sampling in several estuaries will provide a temporal proxy of the lice infestation at the given times. Additionally, out-migrating sea trout smolts should be caught and analyzed before they enter the sea. This will provide data of the marine duration from the first sea-entry to the final return up the river.

As previously mentioned, fish having more than 0.45 lice g^{-1} at the day of lice counting did not return. This only accounts for 16.8 % of the analyzed fish experiencing severe lice infestations. The absence of a significant relationship between the number of lice and mass specific intensity on the date of return might therefore be due to a low portion of the examined trout experiencing life threatening infestation rates.

4.3 Preferences among ascending trout

The results suggested that the sea trout preferred to ascend the river during hours where the tide reaches the upper ranges. As the river Heggaelva is a small stream that enters the sea through a shallow littoral zone (Figure 10), the trout may be exposed and vulnerable during their upstream migration. Various species of seabirds such as, grey herons (*Ardea cinerea*) and grey gulls (*Larus argentatus*) were observed scouting for potential prey items at the riverbank during low tide. The higher tidal ranges may therefore be preferred due to a reduced accessibility for sea birds as it reduces the amount of exposed land for the birds to reside. Higher tidal ranges also make the stream deeper which further reduce the accessibility for predators and allows for more potential space the trout can distribute itself in. To validate these assumptions, further studies should map the behavior of residing seabirds in relation to various tidal ranges.

Most of the sampled trout returned during a water temperature range of 11 – 14 ºC compared to the other temperature ranges tested. In a study where the relationship between the metabolism and the water temperature of sea trout was investigated, a temperature range of 8 – 11 °C was proven optimal for maximizing the efficiency of the energy utilization from prey items (Elliott, 1976). They also found the swimming activity to make up 12 % of the total metabolism at 3.8 °C to over 70 % at 17.8 °C (Elliott, 1976). Natural impediments such as swimming against the current and escalating culverts, in addition to a reduction in food availability may increase the depletion rate of the fish's energy storage. Higher water temperature ranges might also cause a rapid depletion of these storages and lead to exhaustion. Another study conducted by Larsson, (2005), found a preference for temperature between 12-17°C for migratory trout dependent on fish size and food availability. These are slightly higher temperatures than what was found at Agdenes. Larsson, (2005) found that the energy cost of swimming increased in relation to the temperature. A temperature range of 8 – 11 °C might therefore be a trade-off between energy cost and potential growth when sea trout ascend the river. Seasonal effects outside the scope of this study might also have triggered the trout to return. For example, a diminishing availability of resources for growth in conjecture with an increasing risk of predation might have made it beneficial to return within the same time span in which the temperatures were 11 – 14 ºC. The preference of temperature might be partly explained by seasonal affects as the temperature range of 11 – 14 ºC was most frequently measured in the estuary.

A significant influence by various light conditions on the timing of the upward migration was not detected. Haraldstad et al., (2017) and Aldvén et al., (2015), both found the probability for a sea trout to descend the river during daytime increased in relation to the river temperature. Temperatures below 10°C increased the probability of the trout to initiate marine migration at night during lower light intensities, according to the findings of Aldvén et al., (2015). The explanation being that higher temperatures closer to optimal would enable the metabolism to allow for greater swimming speeds to escape predators if necessary. Thus, not having to rely on the darkness for camouflage. This behavior might reflect the findings of this study regarding the preference of ascending trout as well. The water temperature was less than 10 °C during less than 8 % of the time in the surveillance period from the 1st of June until the 30th of September. Thus, the trout would in most cases rely on their metabolism and swimming speeds to perform their upward migration. Although insignificant, a trend was present where 62.5 % of the returning trout returned within the time interval 18:01 – 06:00. These were the time intervals with the lowest light intensities during the summer. An undetectable bias toward an upward migration during lower light intensities might therefore still be present.

No preference regarding a particular range of precipitation was found among the returning trout. Jonsson & Jonsson, (2002) found the likelihood of a trout ascending the river to be positively influenced by an increasing water flow up to a given threshold, as it allows for increased maneuverability between obstacles in the river as well as protection against predators. They also found that a water flow above this threshold decreased the likelihood of upstream migrations as it became increasingly energy demanding to swim against the stronger currents. These findings are in agreement with a more recent study where the effect of water flow on the upstream migration movement of brown trout in a regulated river was investigated (García-Vega et al., 2017). However, the finding of these studies does not fit the migration pattern of the trout analyzed in this thesis. The methodological choice of using the precipitation as a proxy for water flow in the river does not necessarily provide accurate measurements as it is an indirect approach of a measurement. The data was also retrieved from a nearby weather station. Direct measurements of the waterflow during the season should be applied in further studies to investigate the relationship between waterflow and the likelihood of a trout ascending at Agdenes properly. It might also be that the effect of the water flow is insignificant unless it becomes so low it prohibits the fish from maneuvering up the river. Conditions like this did not occur during the study season.

5 CONCLUSIONS

- The likelihood of the trout returning to the river increased with body length, possibly due to enhanced swimming speed and endurance of larger trout, thus improving the trout's ability to outswim predators and reduce the risk of predation.
- Sea trout experiencing infestation rates above 0.45 lice g^{-1} did not return to the river. This support hypothesis 1 in this thesis. It is possible that the trout could withstand elevated sea lice infestations up to a certain threshold until it become life threatening and thus reduce the likelihood of the trout returning.
- This thesis shows that this type of studies can be useful to define thresholds for when sea trout do not return after the marine growth phase based on sea lice infestation rates. Such thresholds may be important for operationalization of management strategies, including implementation of sea trout as an indicator species in Trafikklyssystemet. However, it is necessary to repeat these studies over several years for multiple populations.
- Trout which suffered higher sea lice infestations did not return to the river earlier. Consequently, none of the results support hypothesis 2. As data related to the trout's residency time in the estuary are lacking, the trout may have returned prematurely to the brackish areas to delouse themselves. Hence, an effect might still be present which the data was unable to reveal.
- Higher tidal ranges were preferred by sea trout for the upstream migration supporting hypothesis 3 in this thesis. Plausible explanations may be reduced accessibility for terrestrial predators and larger maneuverable water masses for the trout to distribute itself in, provided by a deeper river at high tidal ranges.
- The majority of the trout returned from the sea to the river during a water temperature range of 11 – 14 °C in the estuary supporting hypothesis 3 in this thesis. This finding may possibly be related to a trade-off between the optimal temperature range for energy utilization of the feed and optimal growth.
- This thesis shows that abiotic conditions in the estuary may regulate the timing of the return from sea to freshwater, thus providing new insight for future studies aiming to answer questions related to the migration behavior of returning sea trout.
- Various light conditions were not found to significantly influence the timing of the upward migration. Optimal temperatures for energy utilization during the season as well as high tides may have mitigated the need to rely on the darkness for protection when migrating upstream.
- Various ranges of precipitation were not found to significantly influence the timing of the upward migration, perhaps because waterflow being indirectly estimated by the amount of rainfall.

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7 Appendix 1 – Methodical illustrations and tables

7.1 Figure 18: Expected migration distance and nearby freshwater areas

Figure 18: An 18 km radius from the river Heggaelva illustrating the expected travel distance for migrating anadromous trout in addition to nearby freshwater areas for potential delousing. Source: Unpublished stream survey by NINA.

7.9 Table 1: Dimensions of the fyke net

Table 1: The dimensions was obtained from Marius Berg/NINA

Section	Lenght (meter)	Width (meter)	Height (meter)	Diameter (centimeter
Leading net	25	–	3,5	–
Fyke wings	5	–	3,5	–
Box chamber and opening wedge	5	5	3,5	–
Cone-shaped section between box- and catch chamber	2	2,5 towards box chamber 2 towards the chatch chamber	3,5	–
Cylindrical catch chamber	5	–	–	90
Section	**Mask width (millimeter)**	**Material**	**Additional info**	
Leading net	20	Polyethylene	Possible to add sections to increase lenght	
Fyke wings	20	Polyethylene	–	
Box chamber and opening wedge	20	Polyethylene	–	
Coneshaped- section between box- and catch chamber	–	Polyethylene	A seal-block in the front (0,5m x 0,5m) forming four openings (22,5cm x 22,5 cm)	
Cylindrical catch chamber	15-10	Nylon	–	

7.10 Table 2: Dataset - migration pattern

Table 2: A section of the dataset used to interpret the migration pattern of the trout

Tag ID	Scan Date	Circular lower	Circular upper	Stationary lower	Stationary upper	Direction	Migration purpose	Time after tagging (days)
989,001005590251	20,07,2020			13:36:13	13:52:03	Up	7 days PMR	19
	21,07,2020		12:34:54	00:32:24	03:58:18	Down		20
	23,07,2020		17:55:45	11:28:24	11:20:14	Down		22
	24,07,2020			00:29:17				23
	25,07,2020		03:23:24					24
	26,07,2020		23:38:55	22:15:22	22:12:01	Down		25
	27,07,2020		03:26:40					26
989,001005590252	14,07,2020		20:55:56	22:00:25	22:01:44	Up	Return	14
989,001005590253	30,07,2020		15:46:41	16:54:03	17:08:08	Up	Return	30
989,001005590258	23,08,2020		06:33:54	07:40:05	22:01:11	Up	Return	53
989,001005590260	12,07,2020		19:11:21			Up	Stay in the river for 10 days, stay in the estuary 2 days than return	12
	13,07,2020			00:56:14	01:29:14			13
	21,07,2020				04:41:40			21
	22,07,2020				18:25:21			22
	24,07,2020		04:29:47	05:26:00	17:58:37	Down		24
	25,07,2020		05:25:57	06:14:09	06:06:38	Up		26
	26,07,2020			00:00:34	04:54:43	Up		26
989,001005590263	22,07,2020		14:35:37	15:36:40	15:38:38	Up	Return	21
989,001005590264	08,09,2020		08:00:07	09:04:22	09:12:51	Up	Return	69
989,001005590267	28,08,2020		21:53:18	22:57:17	22:59:29	Up	Return	58
989,001005590269	02,07,2020				22:41:01		?	1
	02,07,2020				22:51:11			

7.11 Table 3: Contingency table for the preferred tidal range

Table 1: The contingency table used to investigate if the returning trout preferred a specific tidal range in a Fisher's Exact Test

Classes	Expected random distribution	Observed distribution	Total
0 – 100 cm	645	7	652
101 – 200 cm	1082	25	1107
201 – 300 cm	779	31	810
Total	2506	63	2569

7.12 Table 4: Contingency table for the preferred precipitation range

Table 1: The contingency table used to investigate if the returning trout preferred a specific precipitation range in a Fisher's Exact Test

Classes	Expected random distribution	Observed distribution	Total
0 – 10mm	78	41	119
10.1 – 20mm	15	14	29
20.1 – 30mm	8	6	14
30.1 – 40mm	3	2	5
Total	104	63	167

7.13 Table 5: Contingency table for the preferred light conditions

Table 1: The contingency table used to investigate if the returning trout preferred specific light conditions in a Fisher's Exact Test

Classes	Expected random distribution	Observed distribution	Total
00:01 – 06:00	26	25	119
06:01 – 12:00	26	9	29
12.01 – 18:00	26	14	14
18.01 – 24:00	26	15	5
Total	104	63	167

7.14 Table 6: Contingency table for the preferred temperature range

Table 1: The contingency table used to investigate if the returning trout preferred a specific water temperature range in a Fisher's Exact Test

Classes	Expected random distribution	Observed distribution	Total

8 – 11 ºC	393	5	398
11.01 – 14 ºC	499	46	545
14.01 – 17 ºC	438	12	450
Total	1330	63	1393

8 Appendix 2 – Test statistics

8.1 Table 9: Outputs

Table 7: The output of each statistical test conducted in this study

Test	Estimate	Standard error	z value	Pr(>|z|)	R-squared	D.f.
GLM (Return ~ Body length)	0.8174	0.1853	4.110	0.0000103	-	190
GLM (Return ~ K-factor)	0.1403	0.1775	0.790	0.429	-	190
GLM (Return ~ Lice)	-0.2092	0.1732	-1.208	0.227	-	190
Linear regression (Immobile lice ~ Days since lice count)	0.1350	0.0733	1.842	0.070	0.0527	61
Linear regression (Mobile lice ~ Days since lice count)	-0.0084	0.0815	-0.103	0.919	0.0002	61
Linear regression (Lice total ~ Days since lice count)	0.1277	0.1361	0.938	0.352	0.0142	61
Linear regression (Immobile lice ~ Day of return)	0.1142	0.0779	1.467	0.148	0.0341	61
Linear regression (Mobile lice ~ Day of return)	0.0219	0.0857	0.255	0.800	0.0011	61
Linear regression (Lice total ~ Day of return)	0.1374	0.1431	0.960	0.341	0.0149	61
Fisher's exact test (Precipitation)	-	-	-	0.5393	-	-
Fisher's exact test (Tide)	-	-	-	0.0027	-	-
Fisher's exact test (Light conditions)	-	-	-	0.1725	-	-
Fisher's exact test (Temperature estuary)	-	-	-	< 0.001	-	-

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